Positive Association Between Densities of the Red Imported Fire Ant, *Solenopsis invicta* (Hymenoptera: Formicidae), and Generalized Ant and Arthropod Diversity

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ABSTRACT The invasive ant, *Solenopsis invicta* Buren, is a threat to native arthropod biodiversity. We compared areas with naturally varying densities of mostly monogyne *S. invicta* and examined the association of *S. invicta* density with three diversity variables: (1) the species richness of ants, (2) the species richness of non-ant arthropods, and (3) the abundance of non-*S. invicta* ants. Pitfall traps were used to quantify *S. invicta* density and the three diversity variables; measurement of mound areas provided a complementary measure of *S. invicta* density. We sampled 45 sites of similar habitat in north central Florida in both the spring and autumn of 2000. We used partial correlations to elucidate the association between *S. invicta* density and the three diversity variables, extracting the effects of temperature and humidity on foraging activity. Surprisingly, we found moderate positive correlations between *S. invicta* density and species richness of both ants and non-ant arthropods. Weaker, but usually positive, correlations were found between *S. invicta* density and the abundance of non-*S. invicta* ants. A total of 37 ant species, representing 16 genera, were found to coexist with *S. invicta* over the 45 sites. These results suggest that *S. invicta* densities as well as the diversities of other ants and arthropods are regulated by common factors (e.g., productivity). Many invaded communities may be more resistant to *S. invicta* than generally believed, or possess an unexpected resilience for recovery if *S. invicta* can be permanently suppressed.

KEY WORDS *Solenopsis invicta*, arthropod diversity, invasive species, partial correlation

INVASIVE ANTS MAY NEGATIVELY impact the diversity of native ants and other arthropods (e.g., Porter and Savignano 1990, Human and Gordon 1997, Jourdan 1997, Holway 1998, Hoffmann et al. 1999, Sanders et al. 2001). One of the most notorious invasive species, the red imported fire ant, *Solenopsis invicta* Buren, has been shown to reduce the species richness and abundance of many native ants and other arthropods. Almost all studies investigating the effects of *S. invicta,* however, have compared communities (Nichols and Sites 1989, Camilo and Phillips 1990, Porter and Savignano 1990, Morris and Steigman 1993, Jusino-Atresino and Phillips 1994, Kaspari 2000, Gotelli and Arnett 2000) or experimental units (Summerlin et al. 1984, Vinson 1991, Stoker et al. 1995) with and without this invader.

Population densities of *S. invicta,* however, may vary greatly (e.g., Diffie and Bass 1994). An issue that has rarely been addressed is the association between varying densities of *S. invicta* and the diversity of ants and other arthropods. The few studies that have compared areas with naturally varying densities of *S. invicta* (i.e., not because of pesticide treatments) found an overall negative association between *S. invicta* density and overall ant species richness and abundance (Stein and Thorvilson 1989, Camilo and Phillips 1990). Very few sites were compared, however, and habitat variation

or degree of disturbance among sites were confounding variables in these studies.

In general, a negative association of *S. invicta* density with overall arthropod diversity would be consistent with the hypothesis that *S. invicta* depresses native arthropod populations. In contrast, a positive association would be consistent with the hypothesis that both *S. invicta* and other arthropod species are similarly affected by some common factor(s). A finding of no association would suggest that *S. invicta* populations are regulated by different factors than those regulating populations of other arthropods.

The prevailing conventional wisdom seems to be that communities with higher densities of *S. invicta* will have lower diversities of arthropods in general (i.e., the first scenario described above). Relatively little data exist to support this idea, however. Thus we conducted a study over a large number of sites of the same habitat type to evaluate the associations of *S. invicta* density with: (1) the species richness of ants, (2) the species richness of non-ant arthropods, and (3) the abundance of non-*S. invicta* ants.

Materials and Methods

Sampling. This study was conducted on pasture land in North Central Florida. Forty-five study sites

were established, between 29° 39′ and 30° 06′ N latitude and between 82° 07′ and 82° 43′ W longitude. Sites were at least 500 m apart, and most were separated by several km. All sites were located in full sun and grazed by cattle or horses, although grazing intensity varied among sites. None of the pastures had any recent history of pesticide use. Chemicals used against fire ants—even older hydrocarbons such as Mirex—have relatively short residual effects (<1 yr; Markin et al. 1974, Summerlin et al. 1977). The monogyne (i.e., single queen) form of *S. invicta* was present at all sites, although some polygyne (i.e., multiple queen) colonies may have been present at some sites. Because *S. invicta* is virtually ubiquitous in open areas in northern Florida, no pastures naturally lacking *S. invicta* were available for comparison.

Fifteen pitfall traps were set out at each site, placed at 8-m intervals in a 3×5 grid. Pitfalls consisted of plastic vials (2.5 cm diameter and 7 cm deep) containing propylene glycol as a preservative. A rechargeable battery-powered drill was used to bore holes of the exact diameter of the vials, which were inserted so that the lip was flush with the ground surface. This method produced a minimal "digging in" effect (Greenslade 1973).

Pitfalls were left out for 72 h. Occasionally pitfalls were disturbed, apparently by small mammals, and these samples were discarded. On rare occasions where >4 pitfalls at the same site were disturbed, all samples from that site were discarded and a new set of pitfalls was set out 1–2 wk later. All samples were stored in a freezer until they could be sorted. Ants were identified to species, and all other invertebrates were identified to at least order (with the exception of classes Chilopoda and Diplopoda) and then sorted as morphospecies. Voucher specimens of ants have been placed in the Florida State Collection of Arthropods in Gainesville, FL.

At each site, plots were established to determine *S. invicta* mound area and number, as a complementary measure of *S. invicta* density. The plots encompassed the pitfall trap grids and enough of the surrounding area so that 20–25 mounds were present in each plot; plots varied in size between 465 and 2,743 m². Larger plots were used at sites with fewer mounds to reduce sampling error associated with possible nonrandom distribution of the mounds.

In each plot, observers walked along transects 3 m wide, marking all mounds in the transects. Two or three observers usually walked in tandem. After the entire plot had been searched in this manner, each mound was measured along its longest axis, and then perpendicular to that axis. The two-dimensional shape of most mounds approximated an ellipse, and the two-dimensional area of the mounds was calculated using the formula for an ellipse ($A = \pi * a/2 * b/2$, where a = length of the longest axis and b = length of the perpendicular axis; as in Macom and Porter 1996). The two-dimensional areas of all mounds in each plot were summed, and this cumulative mound area was divided by the size of the plot to obtain a measure of total mound area (m²) per ha. This variable was used rather than number of mounds per ha because mound size varied greatly.

Each site was sampled in the spring (between 3 and 25 April) and then again in autumn (between 2 October and 9 November) of 2000. Sites were sampled in two different seasons because *S. invicta* abundance and activity may vary seasonally (Porter and Tschinkel 1987, Tschinkel 1988b, 1993). In both seasons, pitfalls were placed in the same positions at each site, and mounds were counted and measured over the same plots.

Because of the large number and spatial distribution of sites, sampling required several weeks. We attempted to sample during similar climatic conditions, but some degree of climatic variation was unavoidable. To control for potential confounding effects of climate, temperature and relative humidity data for the sampling periods were obtained from the NOAA weather station at Gainesville Regional Airport (29° 41′ N, 82° 16′ W; National Climatic Data Center, Asheville, NC). Hourly values for temperature and relative humidity were averaged over all 72-h pitfall trapping periods, for inclusion in partial correlation analyses (see below).

Statistical Analyses. *Solenopsis invicta* density was quantified in three ways at each site: (1) the mean number of *S. invicta* workers per pitfall, (2) the proportion of pitfalls occupied by *S. invicta,* and (3) *S. invicta* total mound area (m²) per ha. Each measure is subject to limitations. For example, large numbers of workers could accumulate in a single pitfall, because of the pitfall being placed fortuitously near a mound or tunnel entrance. The proportion of occupied pitfalls, because of the small potential range of variation, may greatly underestimate the variation in *S. invicta* densities in comparisons among sites. Although mound area is strongly correlated with worker abundance in *S. invicta* (Tschinkel 1993, Macom and Porter 1996), variation in factors such as soil type, soil moisture, and disturbance regime may affect mound morphology across sites.

We examined four variables representing different measures of ant and other arthropod species diversity: (1) ant species richness (mean number of ant species per pitfall), (2) non-ant species richness (mean number of non-ant species per pitfall), (3) non-*S. invicta* ant abundance measured as the mean number of non-*S. invicta* ants per pitfall, and (4) non-*S. invicta* ant abundance measured as the proportion of pitfalls occupied by non-*S. invicta* ants. Note that variables three and four are subject to the same limitations as the measures of *S. invicta* density from pitfalls described above.

Distributions of all variables were examined and transformations were applied when necessary to normalize the data. The mean number of *S. invicta* workers per pitfall and the mean number of non-*S. invicta* ants per pitfall were log10 transformed. The proportion of pitfalls occupied by *S. invicta* and the proportion of pitfalls occupied by non-*S. invicta* ants were arcsine square root transformed. *Solenopsis invicta* total mound area per ha, ant species richness (mean

Table 1. Partial correlations of *S. invicta* density with four measures of ant and other arthropod diversity (*n* = 45 study sites in each season). See text for explanation and rationale of variables

Dependent variable	Spring 2000 R	Autumn 2000 R
S. invicta density as mean number per pitfall		
Ant species richness	0.170	0.389**
Non-ant species richness	0.317*	0.296
Non-*S. invicta* ant abundance (number)	0.112	0.173
Non-*S. invicta* ant abundance (proportion)	0.072	0.249
S. invicta density as proportion of pitfalls occupied		
Ant species richness	0.345*	0.389**
Non-ant species richness	0.406**	0.314*
Non-*S. invicta* ant abundance (number)	0.239	−0.048
Non-*S. invicta* ant abundance (proportion)	0.150	0.129
S. invicta density as mound area (m²) per hectare		
Ant species richness	0.278	0.059
Non-ant species richness	0.451**	0.112
Non-*S. invicta* ant abundance (number)	0.265	−0.118
Non-*S. invicta* ant abundance (proportion)	0.173	−0.005

* Significant at $\alpha < 0.05$; ** significant at $\alpha < 0.01$.

number of ant species per pitfall) and non-ant species richness (mean number of non-ant species per pitfall) were not transformed.

Because foraging activity in ants and other arthropods is affected by temperature and humidity (e.g., May 1985, Wharton 1985, Porter and Tschinkel 1987, Hölldobler and Wilson 1990), we performed partial correlations between *S. invicta* density and each of the four measures of ant and other arthropod species diversity. Partial correlations measure the correlation between two variables when the common variance of other variables (in this case temperature and relative humidity) is extracted (Kachigan 1991). Separate analyses were conducted for all three measures of *S. invicta* density, and for each season of the year (spring and autumn). StatView 5.1 (SAS Institute Inc., Carey, NC) was used for statistical analyses.

Results

Densities of *S. invicta* varied among the 45 sites over a range of up to two orders of magnitude, depending upon the variable of comparison used. In the spring of 2000, the average number of *S. invicta* workers per pitfall ranged from 0.6 to 37; the proportion of pitfalls in which *S. invicta* was trapped ranged from 0.13 to 1.00; and the total mound area per ha ranged from 1.08 to 55.77 m². Similar ranges of densities were obtained for these variables in autumn of 2000 (0.6–14, 0.20–0.93, and 0.83–80.99 m², respectively). The range of variation in total mound area per ha encompasses that reported from other studies of *S. invicta* density (e.g., Macom and Porter 1996, Porter et al. 1997)

All but three partial correlations between *S. invicta* density and the four measures of ant and other arthropod species diversity were positive (Table 1). Temperature and relative humidity were highly positively correlated ($r = 0.88$ and 0.74, spring and autumn, respectively) and partial correlations conducted without the confounding factor relative humidity did not yield qualitatively different results.

Ant species richness was significantly positively correlated with *S. invicta* density in a number of comparisons, particularly in autumn. Non-ant species richness was significantly positively correlated with *S. invicta* density, especially in the spring, when relatively high positive correlations were found regardless of how *S. invicta* density was quantified. Partial correlations between *S. invicta* density and non-*S. invicta* ant abundance (regardless of how measured) were weaker, but usually positive. In general, partial correlations of a small magnitude (<0.3) may not be indicative of meaningful biological associations. Stronger correlations, however, suggest potentially important patterns of community species diversity.

Over all the sites sampled, a total of 37 different ant species, from 16 different genera, were found to coexist with *S. invicta* (Table 2). The number of ant species per pitfall (including *S. invicta*) ranged from 1.3 to 4.6 in the spring and from 0.9 to 3.6 in autumn. Summing over all sites, *S. invicta* was the most abundant ant species (Fig. 1).

A cumulative total of 19 different orders of arthropods were captured in pitfall traps (Table 3). The number of non-ant morphospecies per pitfall ranged from 1.3 to 4.6 in the spring and from 0.9 to 3.6 in autumn.

Discussion

Overall, we observed many positive correlations between *S. invicta* density and the diversity measures of ants and other arthropods. The few negative correlations (three out of 24) were not significant (all $r < 0.12$). This is a surprising finding, given the reputation of *S. invicta* for decreasing arthropod diversity in invaded communities (e.g., Camilo and Phillips 1990, Porter and Savignano 1990, Morris and Steigman 1993, Jusino-Atresino and Phillips 1994). Although this study was one of correlation rather than causation, the positive associations suggest that whatever factors reg-

Table 2.   Number of sites (out of 45) at which the indicated ant species were caught in pitfall traps

Species	Spring	Autumn
Aphaenogaster flemingi Smith	1	0
Aphaenogaster floridana Smith	1	0
Brachymyrmex c.f. *obscurior* Forel	12	6
Brachymyrmex depilis Emery	5	9
Camponotus floridanus (Buckley)	1	0
Cardiocondyla emeryi Forel	6	7
Cardiocondyla nuda (Mayr)	26	27
Cardiocondyla venustula Wheeler	9	11
Cardiocondyla wroughtoni (Forel)	2	2
Crematogaster ashmeadi Mayr	0	2
Crematogaster pilosa Emery	1	0
Cyphomyrmex rimosus (Spinola)	40	33
Dorymyrmex bureni (Trager)	34	38
Dorymyrmex smithi Cole	1	0
Formica pallidefulva Latreille	2	0
Formica dolosa Buren	1	1
Hypoponera opaciceps (Mayr)	14	17
Hypoponera punctatissima (Roger)	1	2
Odontomachus brunneus (Patton)	3	3
Paratrechina sp.[a]	8	8
Pheidole crassicornis Emery	2	2
Pheidole dentata Mayr	2	2
Pheidole metallescens Emery	24	23
Pheidole moerens Wheeler	32	25
Pheidole morrisi Forel	0	1
Pheidole tysoni Forel	1	1
Prenolepis imparis (Say)	1	0
Pyramica eggersi (Emery)	0	2
Pyramica membranifera (Emery)	1	7
Solenopsis c.f. *abdita* Thompson	0	4
Solenopsis c.f. *carolinensis* Forel	23	17
Solenopsis c.f. *pergandei* Forel	0	4
Solenopsis c.f. *picta* Emery	2	0
Solenopsis c.f. *tennesseensis* Smith	0	1
Solenopsis geminata (F.)	1	0
Solenopsis invicta Buren	45	45
Trachymyrmex septentrionalis (McCook)	1	0

[a] May represent more than one species.
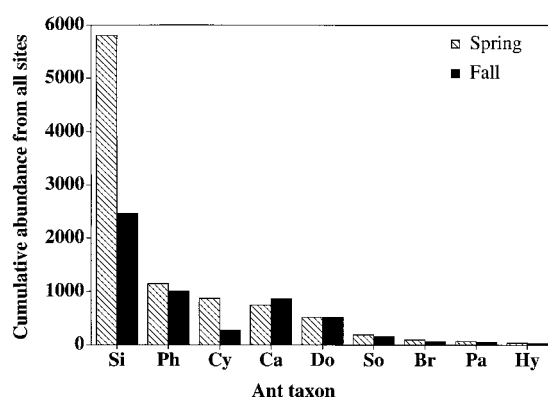
Fig. 1.   Cumulative number of workers caught in pitfall traps from all 45 sites, for *S. invicta* and the eight most abundant genera. Numbers in parenthesis indicate total number of species represented by each genus: Si, *Solenopsis invicta*; Ph, *Pheidole* (6); Cy, *Cyphomyrmex* (1); Ca, *Cardiocondyla* (4); Do, *Dorymyrmex* (2); So, *Solenopsis* (non-*S. invicta*) (6); Br, *Brachymyrmex* (2); Pa, *Paratrechina* (1?); Hy, *Hypoponera* (2). Eight additional genera, each with <50 total trapped workers, are not included here.

ulate overall species diversities also affect *S. invicta* densities to a certain extent.

Several recent studies have revealed that the abundance or species richness of many invaders is often positively correlated with native species diversities (Levine and D'Antonio 1999, Stohlgren et al. 1999). Such positive correlations apparently result from biotic or abiotic factors that covary with native species diversity (e.g., moisture, nutrients, habitat heterogeneity, competitors). Unless native and invasive species differ greatly, the factors controlling native species diversity may also control the abundance or species richness of the invaders (Levine and D'Antonio 1999), as appears to be the case for the sites studied here.

Table 3.   Number of sites (out of 45) at which the indicated arthropod taxa were captured in pitfall traps. Taxa are at the level of order unless otherwise indicated; taxonomy follows Borror et al. (1989)

Taxa	Spring 2000	Autumn 2000
Araneae		
Family Lycosidae	43	44
Family Salticidae	10	8
Other Araneae	45	45
Opiliones	3	2
Pseudoscorpiones	0	1
Isopoda	9	8
Class Diplopoda	16	9
Class Chilopoda	25	13
Collembola	31	35
Orthoptera		
Family Gryllidae	40	43
Family Gryllotalpidae	9	2
Other Orthoptera	15	5
Blattaria	10	17
Isoptera	0	1
Dermaptera	10	20
Psocoptera	20	6
Hemiptera		
Family Lygaeidae	8	23
Family Reduviidae	9	18
Family Cydnidae	17	9
Other Hemiptera	36	15
Homoptera		
Family Aphididae	41	36
Family Cercopidae	4	11
Family Cicadellidae	20	28
Other Homoptera	10	4
Thysanoptera	40	15
Coleoptera		
Family Chrysomelidae	21	11
Family Elateridae	37	38
Family Carabidae	27	28
Family Tenebrionidae	33	31
Family Staphylinidae	36	35
Family Scarabaeidae	31	22
Family Curculionidae	22	27
Other Coleoptera	44	38
Larvae[a]	37	29
Diptera		
Suborder Nematocera	33	38
Suborder Brachycera	34	43
Other Diptera	15	5
Lepidoptera	27	22
Hymenoptera (Non-Formicidae)		
Superfamily Proctotrupoidea	38	33
Superfamily Chalcidoidea	35	25
Other Hymenoptera	13	24

[a] Coleoptera larvae include all families.

Given the complexity of structure and function in most terrestrial arthropod communities (e.g., Price 1997), a number of interacting factors may contribute to the observed positive associations. Inter-site variation in productivity may be an important contributing factor. Wright (1983) proposed that an important determinant of species richness is the productivity of an area, or the rate at which resources are made available to the species of interest. One application of this species-energy theory revealed energy variables to be good predictors of ant abundance over a broad regional scale (Kaspari et al. 2000a, 2000b). Over such large scales, productivity is estimated from variables such as latitude, soil type, temperature, and rainfall (e.g., Kaspari et al. 2000a). Variation in available resources may also exist over smaller, local scales, although accurate quantification of such variation is much more difficult, and may depend upon vagaries in rainfall fluctuations over short distances, soil type, or management regime (including the addition of fertilizers, and grazing pressure). Thus, sites with high diversities of arthropods and corresponding high *S. invicta* densities may also have been more productive.

The magnitude of the observed correlations varied seasonally. When *S. invicta* density was quantified by pitfall traps, relatively stronger positive associations with non-ant species richness were found in the spring, whereas relatively stronger positive associations with ant species richness were found in autumn. There is no obvious explanation for this seasonal variation. Most partial correlation coefficients, however, were not very different between spring and autumn. When *S. invicta* density was quantified as total mound area per ha, stronger positive correlations were found in the spring. Because mound construction by *S. invicta* is important for brood thermoregulation (Porter and Tschinkel 1993), the mound morphology becomes less critical as temperatures rise. Warm temperatures in the summer and early autumn would preclude the need to construct large mounds for this purpose, and the lack of correlation in autumn may be because of this artifact of seasonality.

The data presented here do not suggest that *S. invicta* has had no negative impacts on overall arthropod species diversity in these communities. It is possible that some or all sites had higher diversities before the *S. invicta* invasion. Unfortunately, no preinvasion data exist. The data do reveal, however, that communities with high densities of monogyne *S. invicta* will not necessarily have a depauperate arthropod fauna. Other factors may often be of relatively greater importance in shaping overall community diversity.

Our findings may not be representative of all areas invaded by *S. invicta.* The situation with polygyne populations of *S. invicta* may differ from the patterns described here. Diversity patterns may also vary as a function of habitat. Analogous studies with polygyne populations or in different habitat types would be of comparative interest.

Many ant species are known to coexist with, or even become more abundant in the presence of, *S. invicta* (Baroni-Urbani and Kannowski 1974, Claborn et al. 1988, Stein and Thorvilson 1989, Camilo and Philips 1990, Jusino-Atresino and Phillips 1994, Wojcik 1994). Some ant species, however, (e.g., *S. xyloni* McCook, *S. geminata* [F.], *Pogonomyrmex barbatus* [F. Smith]) have been documented to decline in abundance and even become excluded from their former ranges by *S. invicta* (Wilson and Brown 1958, Porter et al. 1988, Tschinkel 1988a, Hook and Porter 1990, Trager 1991). Similarly, other types of arthropods may also be either positively or negatively impacted by *S. invicta* (Neece and Bartell 1981, Porter and Savignano 1990). Thus the potential impact of invasive species includes not only decreases in species richness, but also changes in species composition. *Solenopsis invicta* may pose a serious threat to a number of relatively rare or threatened species (e.g., Wojcik et al. 2001) and species identities should be considered along with species numbers in determining the overall impact of such invasions.

Although *S. invicta* may have dramatic negative impacts on invaded communities, relatively little is known about how such effects vary across time and space. For example, Porter and Savignano (1990) documented dramatic decreases in ant and other arthropod species richness and abundance shortly after the *S. invicta* invasion of central Texas. In a follow-up study conducted 12 yr later, Morrison (2002) found that, although *S. invicta* was still the most abundant ant, densities of this invader had decreased by an order of magnitude and overall arthropod diversity had returned to near preinvasion levels. Helms and Vinson (2001) reported relatively large numbers of native ant species coexisting with *S. invicta* 10 yr after the invasion in east Texas, although preinvasion data were not available for comparison.

Native arthropod communities may be more resistant or resilient to the *S. invicta* invasion over time or space than generally believed. This is encouraging news for efforts to control *S. invicta* and restore native communities. For example, phorid flies that are parasitoids of *S. invicta* are potential biocontrol agents and are being released across the southeastern United States (Porter 1998, Morrison 2000). In addition to the direct effect of parasitism, these parasitoids may have relatively large indirect effects on their hosts, altering host behavior and placing their hosts at a competitive disadvantage relative to native ants (Morrison 1999). Thus this parasitoid would be expected to have greater overall impacts in areas with more competing ants. Moreover, if *S. invicta* populations could be permanently decreased, by any sustainable means, affected communities may possess an unexpected resilience for recovery toward their preinvasion states.

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